

# Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought

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## Abstract

Catastrophic hydraulic failure will likely be an important mechanism contributing to large-scale tree dieback caused by increased frequency and intensity of droughts under global climate change. To compare the susceptibility of 22 temperate deciduous tree and shrub species to hydraulic failure during a record drought in the southeastern USA, we quantified leaf desiccation, native embolism, wood density, stomatal conductance and predawn and midday leaf water potential at four sites with varying drought intensities. At the two driest sites, there was widespread leaf wilting and desiccation, and most species exhibited predawn leaf water potentials of  $\leq 3$  MPa and  $>60\%$  loss of xylem conductivity in branches. Although species with high wood density were more resistant to cavitation, they had higher levels of native embolism and greater canopy dieback than species with low wood density. This unexpected result can be explained by the failure of species with dense wood to avert a decline in water potential to dangerous levels during the drought. Leaf water potential was negatively correlated with wood density, and the relationship was strongest under conditions of severe water deficit. Species with low wood density avoided catastrophic embolism by relying on an avoidance strategy that involves partial drought deciduousness, higher sensitivity of stomata to leaf water potential and perhaps greater rooting depth. These species therefore maintained water potential at levels that ensured a greater margin of safety against embolism. These differences among species may mediate rapid shifts in species composition of temperate forests if droughts intensify due to climate change.

**Keywords:** cavitation, drought, embolism, hydraulic failure, water relations

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## Introduction

Some of the most severe impacts of climate change may result from an increase in the frequency and intensity of extreme climate events, rather than from gradual changes in mean conditions (e.g. Easterling *et al.*, 2000; Jentsch *et al.*, 2007). Drought, in particular, is likely to become more common in many areas due to increasing temperatures and shifting precipitation (Lehner *et al.*, 2006; Hayhoe *et al.*, 2007). Drought has resulted in tree mortality in many areas of the globe (Fensham *et al.*, 2009; Klos *et al.*, 2009) and has the potential to drive rapid and large-scale shifts in forest structure and species composition under changing climates (Allen & Breshears, 1998; Breshears *et al.*, 2005). Such shifts will be mediated by species differences in drought susceptibility (Mueller *et al.*, 2005), so it is critical to understand the factors that determine these differences.

Drought-induced tree mortality can result from carbon starvation (Adams *et al.*, 2009; Hartmann, 2011), increased susceptibility to pests (Mattson & Haack, 1987; Negrón *et al.*, 2009), or hydraulic failure (Davis *et al.*, 2002; Rice *et al.*, 2004). Hydraulic failure, which may be the primary cause of mortality during acute, short-term drought (McDowell *et al.*, 2008), results when the water in xylem conduits cavitates under high tension. The resulting embolisms impede the transport of water to the canopy, ultimately resulting in death of tissues due to desiccation. This may kill the tree outright, particularly in species incapable of resprouting.

Among species, there is considerable variation in vulnerability to cavitation (Maherali *et al.*, 2004), and it is commonly presumed that species with the most cavitation-resistant xylem are the most successful at avoiding hydraulic failure. This assumption has not been well tested, yet deserves closer scrutiny because avoidance of hydraulic failure also depends on the capacity of plants to regulate plant water potential. Under conditions of modest water deficit, species with the most cavitation-resistant xylem may maintain the greatest margin of safety against hydraulic failure

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(Meinzer *et al.*, 2009), but this trend might be reversed under more severe drought (Jacobsen *et al.*, 2007a). Specifically, it has been argued that species with cavitation-resistant xylem may in fact be more susceptible to hydraulic failure, because these species often exhibit less stringent control of stomata during drought and therefore may allow plant water potential to approach levels at which catastrophic embolism occurs (McDowell *et al.*, 2008). The less stringent control of stomata may be advantageous under chronic, less intense drought, however, because it permits continued carbon assimilation (McDowell *et al.*, 2008).

Susceptibility to hydraulic failure may be strongly linked to wood density, which is functionally related to a suite of traits that govern drought response. Dense wood is typically resistant to embolism (Hacke *et al.*, 2001a; Jacobsen *et al.*, 2007b; Willson *et al.*, 2008) but incurs costs associated with low hydraulic conductivity (Meinzer *et al.*, 2008a), low capacity for water storage (Scholz *et al.*, 2007; Meinzer *et al.*, 2008a), and greater construction cost. Furthermore, species with dense wood tend to maintain lower water potentials (Ackerly, 2004; Bucci *et al.*, 2004; Meinzer *et al.*, 2008a) and might consequently operate with smaller margins of safety against embolism, thereby increasing the risk of hydraulic failure under severe drought. Thus, although wood density is strongly correlated with a suite of traits related to drought response, it is not yet clear whether it is universally correlated with drought resistance.

We compared the responses of 22 tree and shrub species to a record drought in central North Carolina, USA, to identify causal relationships that underlie species differences in hydraulic failure and canopy dieback. The 6-month period (June–November 2007) before and including the initial portion of this study was the driest on record (since 1895) for North Carolina (total precipitation of 446 mm vs. mean of 674 mm), while being the 4th hottest on record. August 2007, the month preceding the study, was the driest (49 mm vs. mean of 135 mm) and second hottest on record (daily means of 26.9 °C vs. 24.5 °C). **We quantified wood density, leaf desiccation, native embolism, stomatal conductance and predawn and midday water potentials in 2007 during the drought and also under near-average conditions in 2008.** The study was conducted in four sites that exhibited a wide range of drought conditions at the peak of the 2007 drought (Table 1).

## Methods

### Study sites and conditions

In September 2007, at the peak of the drought, we chose four study sites in Wake County, NC that spanned a range of visible

drought impacts (Table 1). At two of these sites, Hemlock Bluffs Nature Preserve and the Fred G. Bond Metro Park, trees and shrubs exhibited widespread wilting, desiccation of foliage (Fig. 1), and substantial mortality. In contrast, Lake Raleigh Woods was chosen for comparison because there were few visible signs of drought. A fourth site, Swift Creek Bluffs, exhibited intermediate drought effects, with widespread wilting but little desiccation or tree death. Data from seven meteorological stations distributed in the vicinity did not reveal patterns in precipitation that could explain the site differences in drought impacts; greater plant water deficits at HB and BP are likely caused by shallower soils that overlie paralithic bedrock at depths of 80–100 cm.

In 2007, data were collected over a period of 10 weeks, from 6 September through 15 November. The most severe water deficits occurred from 6 September to 13 September. This was followed by a moderate alleviation of drought conditions resulting from a rainfall event of 39 mm on 14–15 September. Drought conditions had effectively ended by 27 October, following several days during which 142 mm of rainfall were recorded. The measurements performed in 2007 were repeated in September and October of 2008. In 2008, conditions were similar to the long-term mean for June–November; rainfall was 6% below average and mean temperature was 0.4 °C below average.

To minimize effects of microsite differences, we restricted sampling to small areas. At our driest sites we sampled plants within areas of approximately 0.2 ha (Hemlock Bluffs) and 0.13 ha (Bond Park). Within these areas, we observed no obvious patterns in the distribution of species or drought impacts to suggest that microsite differences may have been responsible for the interspecific variation in species response to drought.

We sampled the tree and shrub community to quantify mortality and canopy dieback at the two sites exhibiting the most severe drought impacts. Along transects of variable length, we measured stem height for all trees and shrubs over 1 m tall, and two observers provided independent visual estimates of canopy dieback, quantified here as of the percentage of desiccated (dead) leaf area. For species underrepresented in the transects, we sampled additional individuals outside the transects. An individual was scored as dead if all leaves were recently desiccated, there was no evidence of living branches, and a shallow cut into the trunk revealed dried inner bark and cambium. We consider this as 'apparent' mortality, since we did not subsequently evaluate these individuals for basal resprouting.

### Native embolism and wood density

We measured percent loss of conductivity (PLC) of excised stems to quantify native embolism for a subset of common species at the sites following the approach of Sperry *et al.* (1988). For 18 species (Table S1), this was measured at one or both of the two driest sites, as well as at the most mesic site. These measurements were performed during the drought of 2007 and were repeated in September–October 2008. In 2007, measurements were made during the period of intermediate

**Table 1** Characteristics of the four study sites in Wake County, NC, USA. Water potentials and stomatal conductances represent multi-species means from all measurements taken during the period of most severe drought (6–13 September 2007)

Site	Location	Widespread wilting	Widespread leaf desiccation	Predawn water potential (MPa)	Midday water potential (MPa)	Midday stomatal conductance ( $\text{mmol m}^{-2} \text{s}^{-1}$ )
1	Lake Raleigh Woods	No	No	−1.2	−1.8	37.4
2	Swift Creek Bluffs	Yes	No	−1.9	−2.1	32.4
3	Hemlock Bluffs	Yes	Yes	−2.7	−3.0	20.6
4	Bond Park	Yes	Yes	−3.9	−4.3	10.9

**Fig. 1** Examples of leaf desiccation in (a) *Cornus florida*, (b) *Quercus rubra*, (c) *Fagus grandifolia* and (d) *Viburnum rafinesquianum*.

drought intensity, after the first rainfall event (39 mm) but before the drought-breaking rains (142 mm). Additionally, for *Cornus florida*, *Quercus rubra*, and *Viburnum rafinesquianum*, we examined temporal changes in PLC at the driest sites by performing measurements of native PLC during peak drought conditions (before any rain), several days after the first rainfall event, and several days after the second rainfall event.

Native PLC was measured on branches collected from 5 to 8 individuals per species at a site. These were collected within one hour of sunrise, with care taken to avoid entry of emboli. The first (terminal) cut was performed with the branch submerged in water. The branch was then cut from the plant and immediately recut under water. Any remaining side branches were removed by cutting underwater to eliminate all leaves from the sample. The branches were transported to the laboratory with one end submerged in water, and the other tightly wrapped in an opaque plastic bag. In the laboratory, the branches were again cut under distilled water to remove at

least 25 cm from each end, leaving an unbranched segment 15–20 cm in length and with xylem diameter between 2.8 and 9.7 mm. The branch was connected to a hydraulic apparatus to measure its hydraulic conductance. Deionized water was used as the perfusion liquid with an applied pressure of 5 kPa, a pressure at which we did not observe flushing of embolisms during measurement. We then removed embolisms by flushing with deionized water under a pressure of 100 kPa for at least 2 h. Hydraulic conductivity was measured at two or more intervals during flushing to ensure that conductivity had stabilized. To determine wood density, a 5-cm segment of the stem was split to remove the bark and pith before determining fresh volume using the water displacement method. The sample was then dried to constant mass at 70 °C and weighed.

Native PLC was calculated as  $\text{PLC} = (1 - k_n/k_m) \cdot 100$ , where  $k_n$  is the native conductivity measured before flushing, and  $k_m$  is maximum conductivity measured after embolisms are eliminated. Maximum sapwood-specific conductivity and

leaf-specific conductivity were calculated according to Tyree & Ewers (1991). Leaf area of the excised stem was determined with a CI-202 leaf area meter (CID, Camas, WA, USA). The stem segment was perfused with methylene blue solution before determining the cross-sectional area of active xylem.

### *Vulnerability to cavitation*

We compiled information on vulnerability to cavitation for each diffuse-porous species used in this study to test for relationships between wood density and vulnerability and to calculate the margin of safety against embolism. Vulnerabilities of ring-porous species were not compiled, because their vulnerability curves differ fundamentally from diffuse-porous species (Li *et al.*, 2008), resulting from cavitation of large-diameter early-wood vessels under very modest tension. Thus vulnerability curves of ring-porous are not directly comparable to diffuse-porous species, and we limited our compilation of xylem vulnerability to diffuse-porous species. When possible, we obtained information on vulnerability from the literature (Maherali *et al.*, 2006; Abit, 2008), but for the remaining species we used the air-injection method (Sperry *et al.*, 1996) to measure vulnerability. In 2009, a nondrought year, we collected branches of similar diameter to those used for measurements of native embolism and positioned them within double-ended chambers. Branches were cut to lengths of 25 cm and were flushed with degassed and deionized water for 20 min under a pressure of 0.1 MPa to remove emboli. We successively pressurized the chamber in 1 MPa increments to a maximum pressure of 7 MPa. Each pressure was maintained for 15 min and then released. Before measurement of hydraulic conductance the stem was allowed to decompress as needed to avoid spurious water flow resulting from air expansion within the stem. The first pressure increment (1 MPa) did not result in sizable decreases in conductance for any species (Figure S4), which would have been evidence of cavitation fatigue (Hacke *et al.*, 2001b), so we used the initial conductance measurement as  $k_m$  for calculating PLC. We obtained curves for five to eight branches per species. For each species, we fitted an exponential sigmoidal equation to the relationship between PLC and water potential to estimate the water potential at which 50% PLC ( $P_{50}$ ) is reached.

### *Leaf water potential and stomatal conductance*

Leaf water potential and stomatal conductance of the study species were measured at the peak of the drought in mid-September 2007 and at two dates of progressively increasing water availability (late September and late October 2007), as well as in September 2008. Predawn and midday water potentials were measured for three to five individuals of each species per site at each of these times with a pressure chamber (Model 1000, PMS Instruments, Corvallis, OR, USA). At midday, before excising the leaf for water potential measurement, its abaxial stomatal conductance was measured with an AP4 porometer (Delta-T, Cambridge, UK). The porometer was calibrated on site before measurements, and the chamber humidity was set at ambient values.

### *Chlorophyll fluorescence*

We measured the effect of water deficit on maximum quantum yield of photosystem II ( $F_v:F_m$ ) during the period of most intense drought with a PAM-2100 fluorometer (Heinz Walz GmbH, Effeltrich, Germany). These measurements were performed before dawn to provide a measure of chronic photo-inhibition (e.g. Valladares & Pearcy, 2002). Measurements were performed on two leaves per individual for three to nine individuals per species on the same dates as measurements of predawn and midday water potential. These were performed with a measuring light frequency of  $600\text{ s}^{-1}$  and a saturating pulse of 1 s duration.

### *Analysis*

Standardized major axis (SMA) regression was used to characterize the relationship between leaf water potential and stomatal conductance using SMATR 2.0 (Warton *et al.*, 2006). SMA was used instead of ordinary least squares, because it is not possible to functionally assign either  $g_s$  or  $\psi_L$  as a dependent variable, owing to a negative feedback between the two variables. Before analysis,  $g_s$  was ln-transformed to achieve normality. We used logistic regression to test for effects of size on stem mortality at the two driest sites. To test for an effect of wood density on mortality across species, we used a general linear model with binomial error structure and a logit link function.

We used ordinary least squares regression to test for trait correlations across species. To ensure that these correlations were not spuriously caused by phylogenetic nonindependence, we also tested the relationships using phylogenetically independent contrasts (Felsenstein, 1985). The phylogeny of species was obtained from the APG3 megatree using the Phylomatic utility (Webb & Donoghue, 2005). This did not resolve relationships among the *Viburnum* spp., so we referred to Winkworth & Donoghue (2005) for this information. We used the PDAP 1.15 package (Midford *et al.*, 2005) of Mesquite 1.73 (Maddison & Maddison, 2006) to test for correlations among traits with phylogenetically independent contrasts (PICs). All branches of the phylogeny were scaled to a length of 1.

### *Results*

By early September 2007, trees and shrubs at the two driest sites exhibited widespread wilting, leaf desiccation (Fig. 1), and stem death. Approximately 29% of tree leaf area had desiccated and 7% of stems > 1 m tall had complete desiccation of foliage and were apparently dead. Stem height was not correlated with percent of desiccated leaf area ( $r^2 < 0.01$ ,  $P = 0.87$ ) nor probability of apparent mortality ( $\chi^2 = 1.53$ ,  $P = 0.12$ ). Among species there was no effect of wood density on apparent mortality ( $\chi^2 = 0.41$ ,  $P = 0.52$ ), though highest mortalities were observed for *C. florida* (21%,  $n = 14$ ) and *Viburnum acerifolium* (20%,  $n = 30$ ), both which have wood density  $\geq 0.65\text{ g cm}^{-3}$  (Table S1). Most species

exhibited some dieback of entire branches (particularly *Prunus serotina* and *Oxydendrum arboreum*), but most desiccated leaf area was associated with living branches (personal observation).

At the two driest sites, mean PLC ranged from 16% in *Nyssa sylvatica* to 93.5% in *Fagus grandifolia* and *Fraxinus americana* (Fig. 2). At these sites, 45% of stem samples from diffuse-porous species had PLC values exceeding 80%, while among ring-porous species, 67% of stems exceeded this level of embolism. There was no evidence of seasonal recovery of xylem conductivity in any of the three species for which we measured PLC over a period of lessening drought conditions in 2007 (Table S2). In the following nondrought year, recovery of conductivity was evident in the two diffuse-porous species (*C. florida* and *V. rafinesquianum*), but the ring-porous species (*Q. rubra*) exhibited only a modest increase in conductivity (Fig. 2).

Among species, PLC was positively correlated with percent desiccated leaf area (partial  $r^2 = 0.54$ ,  $P = 0.0005$ , Fig. 3). The relationship was confirmed when tested with phylogenetically independent contrasts (PICs,  $r^2 = 0.38$ ,  $P = 0.004$ ). After accounting for PLC, diffuse-porous species had greater desiccated leaf area than ring-porous species (ANCOVA:  $F_{1,16} = 10.32$ ,  $P = 0.005$ ).

At the two driest sites, species with dense wood tended to be more heavily embolized than species with low wood density, despite possessing xylem that is more resistant to cavitation. Specifically, wood density was strongly and positively correlated with native PLC ( $r^2 = 0.50$ ,  $P = 0.0007$ , Fig. 4a), and percent of leaf area desiccated ( $r^2 = 0.45$ ,  $P = 0.005$ , Fig. 4b). After accounting for wood density with ANCOVA, ring-porous species had less desiccated leaf area than diffuse-porous species ( $F_{1,18} = 7.78$ ,  $P = 0.01$ , Fig. 4b). Among diffuse-porous species,  $P_{50}$  was negatively correlated with wood density ( $r^2 = 0.64$ ,  $P = 0.0006$ , Fig. 5b) and with PLC ( $r^2 = 0.39$ ,  $P = 0.02$ , Figure S1). All of these correlations continued to be significant when tested with PICs.

At the two driest sites, six species (Table S1) experienced substantial reductions in leaf area through a process of gradual leaf senescence. In contrast to the leaf desiccation mentioned above, leaf senescence was characterized by a gradual loss of pigmentation and resorption of N and P (Marchin *et al.*, 2010). These species lost as much as 70% of their leaf area due to senescence by early September 2007, a behavior not observed under nondrought conditions of September 2008 or 2009. At the two driest sites, these partially drought-deciduous species exhibited less desiccated leaf area (6% vs. 31%,  $t_{18} = 4.19$ ,  $P = 0.0005$ , not shown) and lower PLC (44% vs. 75%,  $t_{17} = 3.66$ ,  $P = 0.002$ , Fig. 4) compared with other species. Drought-deciduous

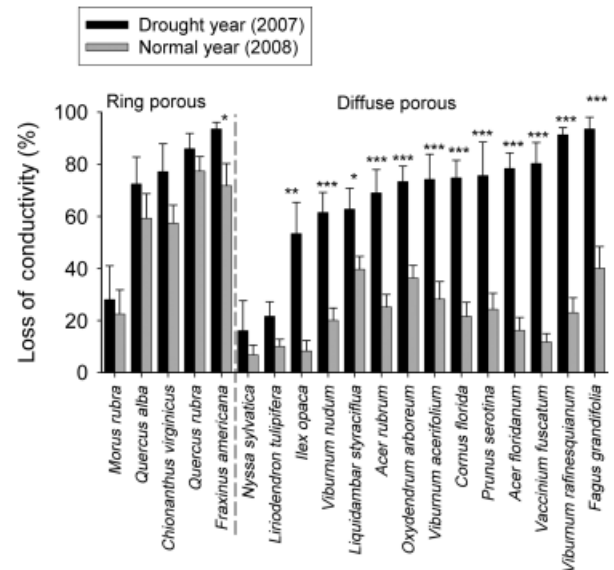


Fig. 2 Mean levels of native embolism for 19 species at two sites severely impacted by drought. Symbols indicate significantly different means between years (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.005$ ). PLC was significantly higher in the drought year than in the non-drought year ( $t_{18df} = 7.60$ ,  $P = 2.5 \times 10^{-7}$ ). Ring-porous species had higher mean PLC than diffuse-porous species during the nondrought ( $t_{17df} = 4.78$ ,  $P = 0.0002$ ) but not the drought year ( $t_{17df} = 0.92$ ,  $P = 0.39$ ).

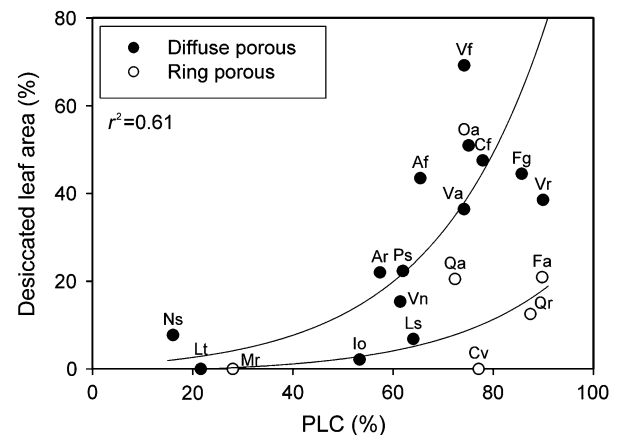
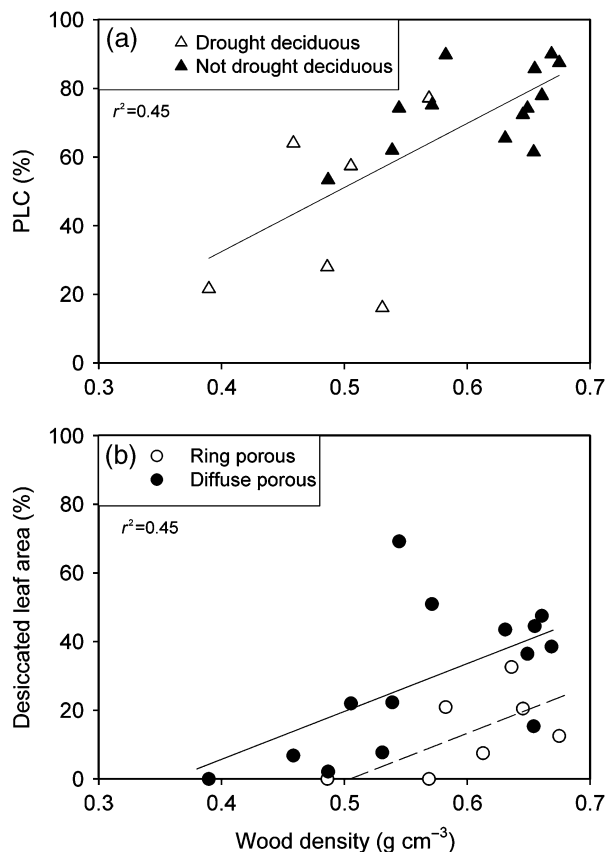


Fig. 3 Relationship between native percent loss of conductivity (PLC) and leaf desiccation at the most severely droughted sites. Curves were fitted with ANCOVA performed on y values transformed as  $\ln(y + 1)$ . There were significant effects of both PLC ( $P = 0.0005$ ) and xylem type (ring porous vs. diffuse porous,  $P = 0.005$ ) on leaf desiccation, but no interaction between these factors ( $P = 0.91$ ). Species codes: Af, *Acer floridanum*; Ar, *Acer rubrum*; Cf, *Cornus florida*; Cv, *Chionanthus virginicus*; Fg, *Fagus grandifolia*; Io, *Ilex opaca*; Ls, *Liquidambar styraciflua*; Lt, *Liriodendron tulipifera*; Mr, *Morus rubra*; Ns, *Nyssa sylvatica*; Oa, *Oxydendrum arboreum*; Ps, *Prunus serotina*; Qa, *Quercus alba*; Qr, *Quercus rubra*; Va, *Viburnum acerifolium*; Vf, *Vaccinium fuscum*; Vn, *Viburnum nudum*; Vr, *Viburnum rafinesquianum*.



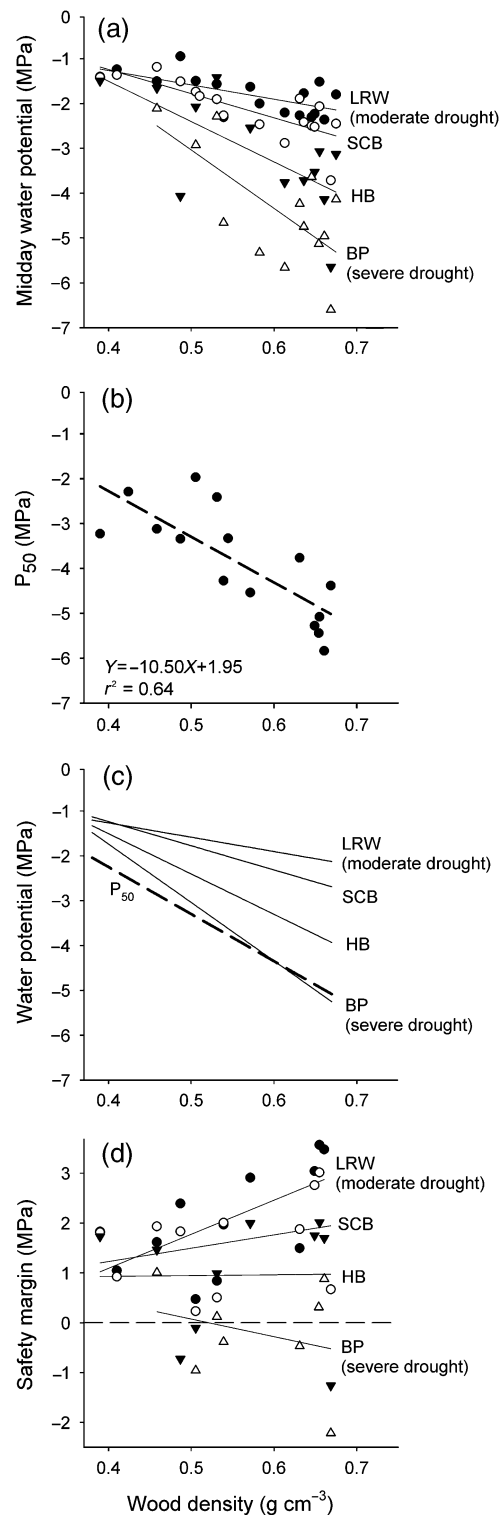


**Fig. 4** (a) Relationship between wood density and native embolism of species at the most severely droughted sites. Species indicated as drought deciduous exhibited substantial leaf loss in a process that involved gradual loss of pigmentation followed by abscission, while the remaining species did not. These partially drought-deciduous species included *Liriodendron tulipifera*, *Nyssa sylvatica*, *Liquidambar styraciflua*, *Chionanthus virginicus*, *Acer rubrum*, and *Morus rubra*. (b) Relationship between wood density and mean leaf desiccation. Lines were fitted with ANCOVA. There were significant effects of both wood density ( $P = 0.005$ ) and xylem type (ring porous vs. diffuse porous,  $P = 0.012$ ), with no interaction between factors ( $P = 0.80$ ).

species also had lower wood density than species that were not drought deciduous ( $0.48$  vs.  $0.61$  g cm<sup>-3</sup>,  $t_{20} = 5.02$ ,  $P = 0.00003$ , Fig. 4).

Wood density was negatively correlated with leaf water potential at midday (Fig. 5a) and before dawn (Figure S2). This relationship was strongest under the most extreme drought conditions, being steepest at the driest sites (Figs 4a, S2) and, within sites, at times of greatest water deficit (Figure S2). This trend arose because species with dense wood were strongly anisohydric, a behavior defined by a large decline in midday water potential during drought. This decline in water potential continued to such an extent under severe drought that these species maintained little or no margin of safety against cavitation, since midday water

potentials tended to approach or drop below  $P_{50}$  (Fig. 5c). Wood density was positively correlated with safety margin at the site with the least severe drought conditions ( $r^2 = 0.43$ ,  $P = 0.01$ ), but the relationship became progressively weaker and nonsignificant under increas-



ingly severe drought conditions due primarily to declining safety margins in species with high wood density (Fig. 5d). Similarly, there was a negative relationship between safety margin and  $P_{50}$  under moderate drought conditions ( $r^2 = 0.87$ ), but this relationship became weaker under increasing severity of drought (Figure S3).

There was substantial variation among species in the sensitivity of stomata to water potential. In species with low wood density, stomata closed abruptly with decreasing water potential, in contrast to the more gradual closure in species with high wood density (Fig. 6). The sensitivity of stomata to water deficit, as quantified by the slope of the relationship between  $\ln(g_s)$  and leaf water potential, was strongly and negatively correlated with wood density (Fig. 6b). We found no relationship between wood density and maximum hydraulic conductivity scaled by sapwood area ( $r^2 = 0.02$ ,  $P = 0.53$ ) or leaf area ( $r^2 < 0.01$ ,  $P = 0.88$ ). When ring-porous species were excluded, these results were unaffected ( $r^2 < 0.03$ ,  $P > 0.54$ , results not shown).

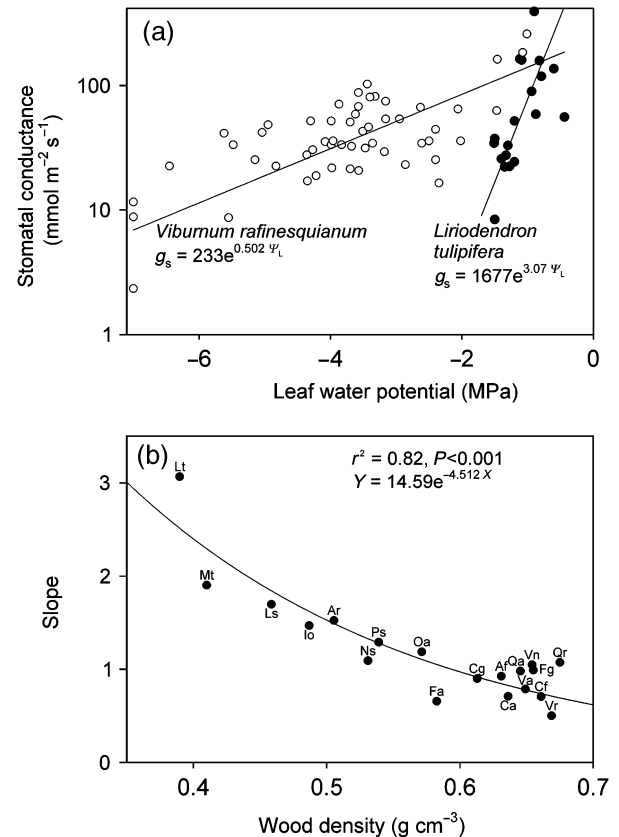
During the drought, predawn  $F_v:F_m$  was significantly and positively correlated with both predawn ( $r^2 = 0.528$ ,  $P < 0.0001$ ) and midday water potentials ( $r^2 = 0.351$ ,  $P = 0.002$ , Fig. 7). The relationship arose primarily from a drop in  $F_v:F_m$  for water potentials below  $-4$  MPa; above this value, water potential appeared to have little or no affect on  $F_v:F_m$ . No species exhibited a mean predawn  $F_v:F_m$  below 0.66 at any site, indicating only modest levels of chronic photoinhibition of photosystem II, despite widespread wilting.

## Discussion

We found that species with dense, cavitation-resistant wood were highly susceptible to hydraulic failure under severe drought conditions, in comparison with species with low wood density. Species with dense

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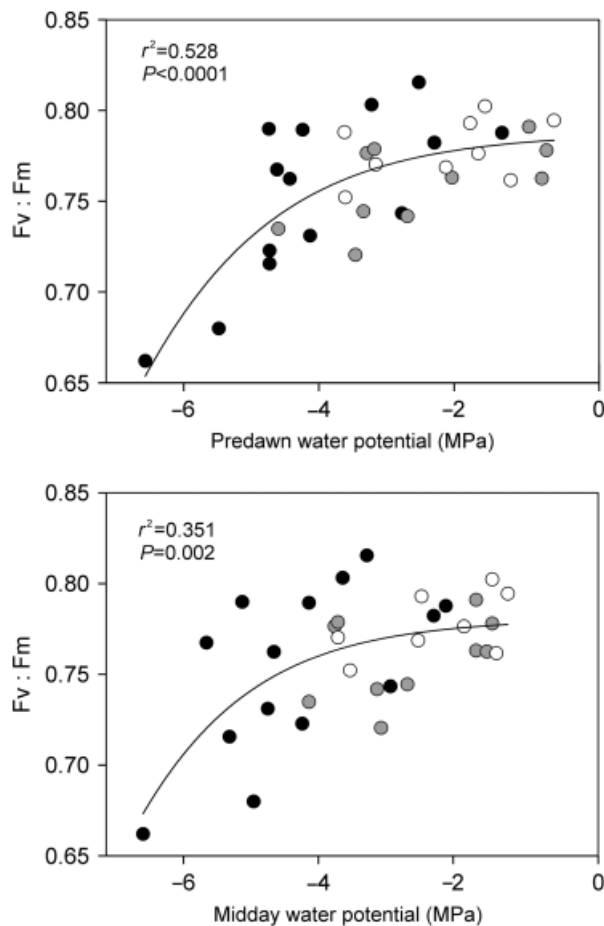
**Fig. 5** (a) Relationship between wood density and midday leaf water potential for four sites. Water potentials were measured during the most intense drought period studied, before any rain. (b) Relationship between wood density and  $P_{50}$  for diffuse porous species.  $P_{50}$  is the xylem water potential at which 50% loss of conductivity is observed. The relationship was confirmed with phylogenetically independent contrasts ( $r^2 = 0.54$ ;  $P = 0.001$ ). (c) The fitted relationships from (a) and (b), superimposed to show the declining margin of safety for species with dense wood under increasing severity of drought. (d) The mid-day safety margin against excessive embolism ( $\psi_{md} - P_{50}$ ), calculated for diffuse-porous species. Species with dense wood tended to have the greatest safety margin under modest drought but little or no safety margin under severe drought. Site codes, in order of increasing water deficit are LRW, Lake Raleigh Woods; SCB, Swift Creek Bluffs; HB, Hemlock Bluffs; BP, Bond Park.



**Fig. 6** (a) Relationship between water potential and stomatal conductance for two species representing extremes in wood density and stomatal control. (b) Relationship between wood density and stomatal sensitivity to water deficit (i.e. the slope of the relationship between water potential and stomatal conductance). Species codes are as in Fig. 3; additional species are included here (*Magnolia tripetala*, Mt; *Carya alba*, Ca; *Carya glabra*, Cg) for which native embolism was not measured.

wood exhibited more extensive embolism and leaf desiccation (Fig. 4), while the two species with the highest whole-plant mortality (*C. florida* and *V. acerifolium*) were among the species with the densest wood (Table S1). These findings are somewhat counterintuitive, considering the strong tendency for dense wood to be more resistant to cavitation than light wood (Fig. 5b, Hacke *et al.*, 2001a; Jacobsen *et al.*, 2007b; Hao *et al.*, 2008; Willson *et al.*, 2008).

This apparent inconsistency can be explained by differences among species in the regulation of plant water potential during drought. Species with dense wood exhibited strong anisohydric behavior, manifested as large declines in leaf water potential during drought (Fig. 5). In these species, midday water potential dropped to such low levels in the driest sites that there remained little or no margin of safety against cavitation (Fig. 5c,d). In contrast, species with low wood



**Fig. 7** Relationship between water potential and the maximum quantum yield of PSII ( $F_v:F_m$ ) measured during peak drought conditions. Each point represents a species mean at a site. Symbol colors correspond to sites with different drought severity: Black, Bond Park (most severe); gray, Hemlock Bluffs; white, Swift Creek Bluffs (least severe). The fitted equations are (top)  $Y = 0.788 / (1 + e^{-0.614 \times -5.620})$  and (bottom)  $Y = 0.780 / (1 + e^{-0.685 \times -6.359})$ .

density maintained high leaf water potentials even at the driest sites. In short, species with dense, cavitation-resistant wood tended to be less successful in maintaining plant water potential at safe levels, and therefore were subject to extensive embolism, despite possessing xylem that is resistant to cavitation. This was likely exacerbated by the low water-storage capacity of dense wood (e.g. Scholz *et al.*, 2007; Meinzer *et al.*, 2008b), which can protect stems by buffering them against rapid declines in plant water potentials occurring at time scales shorter than the response of stomata (Phillips *et al.*, 2004; Meinzer *et al.*, 2008a).

In apparent contrast to our results, Meinzer *et al.* (2009) found that species with dense wood and low midday water potentials maintained the largest margin of safety against cavitation. In that synthesis, however,

data were compiled for plants experiencing seasonal water deficits typical for their respective environments, while we studied plants exposed to a record drought. In fact, at our most mesic site (LRW), which is more representative of the moderate deficits studied by Meinzer *et al.* (2009), our results are in agreement with that study, since safety margins were significantly correlated with wood density (Fig. 5d) and  $P_{50}$  (Figure S3). Under severe drought conditions, these correlations disappeared or even reversed (Figs 5d, S3), as a result of the large declines in midday water potential in these species (Fig. 5c).

A negative relationship between wood density and midday water potential has been observed in diverse systems (Ackerly, 2004; Bucci *et al.*, 2004; Meinzer *et al.*, 2008a; Gotsch *et al.*, 2010), indicating that species with dense, cavitation-resistant wood may be characteristically anisohydric. If so, it may be a widespread phenomenon for species with relatively cavitation-resistant wood to be susceptible to hydraulic failure under severe drought. Unfortunately there have been few comparative studies that can confirm or refute the generality of this result, yet evidence indicates that this is not a spurious occurrence. In woodlands of western US, for example, *Juniperus osteosperma* has denser and more cavitation-resistant wood than *Pinus edulis*, yet the former becomes more heavily embolized because of strong anisohydric behavior (West *et al.*, 2008). Similarly, in chaparral Paddock (2006) observed highest rates of drought-induced mortality in species possessing the most cavitation-resistant xylem. These examples corroborate our finding that species with the most cavitation-resistant wood are the most susceptible to hydraulic failure, at least under some situations. To understand how generally this is true, we must understand the mechanisms that control anisohydry.

Multiple traits may contribute to anisohydric behavior in species with dense wood, including low hydraulic conductance (Meinzer *et al.*, 2008a; Gotsch *et al.*, 2010), shallow root systems (Ackerly, 2004), and weak control of transpiration (McDowell *et al.*, 2008). We lack data on whole-plant hydraulic conductance of most of our study species, but Domec *et al.* (2010) found that whole-plant conductance of *Liquidambar styraciflua* (a species with low wood density) is five-fold greater than *C. florida* (a species with dense wood). Among the full set of study species, we found no correlation between wood density and leaf-specific hydraulic conductivity in terminal branches (data not shown), though this represents only a small component of the whole-plant conductance. More data are needed to evaluate the role of hydraulic conductance in determining the relationship between wood density and midday water potential in our study species.



Shallow root systems likely contribute to the anisohydric behavior of species with dense wood. Some of the study species with dense wood and low midday water potentials possess shallow root systems, such as *C. florida* (Hinckley *et al.*, 1981), *V. rafinesquianum*, *Vaccinium fuscatum* (Gough, 1994) and *Acer saccharum* (Hinckley *et al.*, 1981), which is sometimes considered to be synonymous with our study species, *A. floridanum*. Additionally, species with dense wood had lower predawn leaf water potentials (Figure S2), again suggesting shallower root systems. Inferring relative rooting depth from leaf water potential, however, requires the assumption that leaves have reached equilibrium with soil water potential. This is not reasonable if the conductance of the soil-to-leaf pathway is low (Donovan *et al.*, 2001), as occurs when xylem is heavily embolized, so the predawn water potentials do not provide unequivocal evidence that species with dense wood have consistently shallow roots. In fact, some study species with dense wood are known to have deep roots, including *F. grandifolia*, *Q. rubra*, and *Quercus alba* (Hinckley *et al.*, 1981; Stone & Kalisz, 1991), so rooting depth is likely not the sole factor controlling anisohydric behavior.

The anisohydric behavior of species with dense wood may be explained, at least in part, by their weak controls over leaf area and stomatal conductance. In these species, stomatal conductance was much less sensitive to water potential, compared with species with low wood density (Fig. 6), while species with low wood density tended to exhibit partial drought deciduousness (Fig. 4). This drought deciduousness was under control by the plant, as indicated by a gradual decline in pigmentation and resorption of N and P before abscission (Marchin *et al.*, 2010). This contrasts with leaf desiccation, which was extensive in species with dense wood, but which was characterized by necrosis of leaf blades (Fig. 1) and no evidence of N resorption, relative to healthy leaves (Marchin *et al.*, 2010). Desiccation therefore resulted in a substantial loss of the nutrient capital of leaves that otherwise would have been resorbed by the plant (Marchin *et al.*, 2010).

It is noteworthy that much of the canopy dieback in this study was manifested primarily as desiccation of leaves, with much lower incidence of stem or whole-plant mortality. This is consistent with observations that leaves tend to be more vulnerable to cavitation than stems (Hao *et al.*, 2008; Brodribb & Cochard, 2009), a pattern which should confine damage to leaves while protecting stems (Zimmermann, 1983; Tyree & Sperry, 1988). If this hydraulic segmentation did occur, however, it was not sufficient to prevent catastrophic embolism in branches (Fig. 2). In contrast, pre-emptive reductions in leaf area via senescence did contribute successfully to prevent catastrophic embolism. Unlike

leaf desiccation, leaf senescence was not associated with hydraulic failure of branches, though embolism within the leaves may play a role in triggering leaf senescence (Brodribb & Holbrook, 2003).

### Ecological implications

At the two driest sites, mean PLC in terminal branches ranged from 16% to 93.5% among species (Fig. 2). Previous studies with seedlings have demonstrated that 80% PLC in stems may represent a critical level of embolism among diffuse-porous species, above which death is imminent and photosynthesis is unable to recover to predrought levels (Kursar *et al.*, 2009; Resco *et al.*, 2009), though for conifers this point may be reached at 50% PLC (Brodribb & Cochard, 2009). Overall, 44% of stem samples from diffuse-porous species at the two driest sites had exceeded 80% PLC. Among ring-porous species, 78% of stems exceeded this level of embolism, though it must be noted that this group of species tends to exhibit high levels of embolism even under non-drought conditions (Cavender-Bares & Holbrook, 2001; Jaquish & Ewers, 2001). For three species, we measured PLC on three dates over a period of lessening drought conditions in 2007, but there was no evidence of seasonal recovery of xylem conductance (Table S2).

Although our findings might suggest that species with dense, cavitation-resistant wood are poorly suited for coping with severe drought, this conclusion does not conform to the natural distribution of species. For example, arid environments are generally dominated by species with dense, cavitation-resistant xylem (Maherali *et al.*, 2004; Chave *et al.*, 2006; Martinez-Cabrera *et al.*, 2009). In the present study, most of the species possessing dense wood are quite common in xeric forests, including *O. arboreum*, *V. rafinesquianum*, *V. acerifolium*, *Q. alba* and *C. florida* (Schafale & Weakley, 1990). In contrast, many species with low wood density are considerably more typical of mesic forests, particularly *Morus rubra* and *Liriodendron tulipifera* (Schafale & Weakley, 1990).

This incongruity between species distributions and the observed drought response suggests that hydraulic failure of established trees probably occurs only in the most severe of droughts, while other factors are more important in mediating species abundance under moderate water deficit. As seedlings, for example, all species possess shallow roots, so the deficit-avoidance strategy observed here for species with low wood density is not viable (Pratt *et al.*, 2008; Kursar *et al.*, 2009). At this stage when plants are most vulnerable to drought, species that possess dense, embolism-resistant wood should be the most successful at avoiding hydraulic failure (Pratt *et al.*, 2008; Kursar *et al.*, 2009), in contrast to the trend observed here for well-established plants. Because we

limited data collection to individuals >1 m tall, this most drought-sensitive stage was not included in our sampling. In contrast with other studies (Rice *et al.*, 2004; Mueller *et al.*, 2005; Nepstad *et al.*, 2007; Floyd *et al.*, 2009; Zhang *et al.*, 2009), stem height was not correlated with probability of stem death nor percent of leaf area lost by desiccation.

In this study, we have emphasized the role of hydraulic failure, but under mild, chronic drought, tree death may result largely from carbon starvation (McDowell *et al.*, 2008; Hartmann, 2011). During drought, photosynthesis should be more strongly compromised in species with low wood density, due to reductions in leaf area and stomatal conductance, likely making them more susceptible to carbon starvation (McDowell *et al.*, 2008). Although stomatal conductance recovers when adequate soil moisture returns, lost leaf area will compromise carbon gain until a new cohort of leaves is produced, at considerable cost to the plant. In contrast, the anisohydric strategy exhibited by species with dense wood presumably permits continued assimilation under modest water deficits because they retain leaves and maintain transpiration even when leaves have reached water potentials at which stomata would be closed in other species. This reasoning assumes that drought constrains assimilation primarily through stomatal restriction, which may be a reasonable assumption since maximum quantum yield ( $F_v:F_m$ ) was reduced only modestly under severe water deficit (Fig. 7). As was seen here, drought typically does not result in high levels of chronic photoinhibition of PSII, as inferred from predawn depression of  $F_v:F_m$  (Valladares & Pearcy, 2002; Lawlor & Tezara, 2009), though there is some dispute whether this fully characterizes nonstomatal limitation of assimilation under drought (Lawlor & Tezara, 2009).

## Conclusion

Species with dense, embolism-resistant wood may be particularly susceptible to episodes of extreme drought, despite being generally favored under conditions of modest water deficit. These contrasting trends make it difficult to project changes in species composition without better understanding of the mechanistic bases for drought-induced tree dieback. The present study emphasizes the importance of studying whole-tree responses to water deficit in order to reveal responses that cannot be predicted from tissue-level measurements alone. Measuring whole-tree responses is particularly challenging in regions where extreme drought is infrequent, so it is important to take advantage of rare events when trees are at their physiological limits of drought tolerance. Although such severe drought is still

rare in southeastern US, the frequency of drought has increased modestly in recent decades (Karl *et al.*, 2009) and may continue to do so over the next century (Cooter *et al.*, 2000; Sheffield & Wood, 2008).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Relationship between  $P_{50}$  and percent loss of conductance for diffuse-porous species. The relationship was strengthened when tested with PICs ( $I^2 = 0.54$ ,  $P = 0.035$ ).

**Figure S2.** Relationship between wood density and leaf water potential for four sites exhibiting a range in drought stress (a, b); water potentials were measured during the most intense drought period studied. Relationship between wood density and leaf water potential at the driest site, for three dates over a period of lessening drought conditions in 2007.

**Figure S3.** (a) Relationship between  $P_{50}$  and midday leaf water potential for the four sites. Water potentials were measured during the most intense drought period studied, prior to any rain.  $P_{50}$  is the xylem water potential at which 50% loss of conductivity is observed. (b) The midday safety margin against excessive embolism ( $\psi_{md} - P_{50}$ ), calculated for diffuse-porous species. Site codes, in order of increasing water deficit are LRW, Lake Raleigh Woods; SCB, Swift Creek Bluffs; HB, Hemlock Bluffs; BP, Bond Park.

**Figure S4.** Vulnerability curves used to determine  $P_{50}$ , the water potential at which conductivity is reduced to 50% of maximum. Data for the remaining species were obtained from the literature. We also determined maximum vessel length of each of these species. To do this, five branches of approximately 60 cm were flushed with distilled water for 10 min at 100 kPa. One end of the branch was then attached to a source of compressed air at 100 kPa while the other end was progressively shortened by removing sections of 1–2 cm until air was observed to exit the cut end. Only for *Oxydendrum arboreum* did mean maximum vessel length (32.6 cm) exceed the length of the branches used to determine vulnerability (25 cm). For the remaining species, vessel lengths ranged from 11.8 cm (*Viburnum nudum*) to 19.8 cm (*Prunus serotina*).

**Table S1.** Data summary of the study species. *Xylem* is categorized as diffuse porous (DP) and ring porous (RP). *Phenology* is categorized as partial drought deciduous (D) and not drought deciduous (N). Two species, *F. americana* and *P. serotina*, exhibited very limited amounts of leaf senescence during the drought, and are classified here as not drought deciduous. *WD* is wood density.  $PLC_{08}$  and  $PLC_{07}$  are percent loss of conductivity in the non-drought year (2008) and the drought year (2007). *Slope* is the slope of the relationship between  $\ln(g_s)$  and leaf WP. *Midday water potential* are mean values at each site for the period of most intense drought. *Mortality*, *PLC*, and *desiccation* are mean values from the two driest sites (HB and BP).

**Table S2.** Percent loss of conductivity (%) of three species at three dates of lessening drought intensity. There was no evidence of recovery of conductivity by the end of the season despite substantial amelioration of drought conditions. The first sampling date was in the peak of drought conditions, the second date followed a 39 mm rainfall event, and the last date followed several days of rainfall totaling 142 mm.

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